

EXECHONELLA (EXECHONELLIDAE: BRYOZOA,
CHEILOSTOMATA) FROM THE RECENT AND MIOCENE OF
SOUTHERN AUSTRALIA

P. L. COOK¹ & P. E. BOCK²

¹ Honorary Associate, Marine Biology Section, Museum of Victoria, GPO Box 666E, Melbourne, VIC 3001, Australia.

² School of Ecology and Environment, Deakin University, Melbourne Campus, Burwood Highway, Burwood, Victoria 3125. email pbock@deakin.edu.au

COOK, PATRICIA L. & BOCK, PHILIP E. 2004:12:04. *Exechonella* (Exechonellidae: Bryozoa, Cheilostomata) from the Recent and Miocene of southern Australia. *Proceedings of the Royal Society of Victoria* 116(2): 251-268. ISSN 0035-9211.

The cheilostome family Exechonellidae Harmer, 1957 is widely distributed in time and space. The genus *Exechonella* Duvergier, 1924 has a pan-tropical to subtropical distribution from the Eocene to the Recent and is represented by several Australian species from the Tertiary of Victoria and the Recent of the southern and eastern coasts. Some species exhibit a wide range of variation in morphological characters, and one, *Exechonella papillata*, appears to be new, and is described here. Nearly all specimens are encrusting, but one Tertiary Victorian species has erect, cylindrical, branching colonies. Recent samples, from a depth range of 40-190 metres, include large colonies of several thousand zooids. Frontal wall structures include marginal septular pores connecting between the visceral and hypostegal coeloms, and frontal foramina. Avicularia and homologous structures derived from frontal septular pores are illustrated. The structure of the frontal foramina in different populations of Tertiary *E. marginata*, demonstrates a major development of hypostegal coelom not found in other species, but resembling that found in another exechonellid genus, *Stephanopora* Kirkpatrick, 1888.

Keywords: Bryozoa, Cheilostomata, Exechonellidae, *Exechonella*, Australia, new taxa

HARMER (1957: 651) introduced the family Exechonellidae for *Exechonella* alone. He noted the umbonuloid nature of the frontal shield and listed a large number of Indo-west-Pacific localities for material he assigned, principally, to *E. tuberculata* (MacGillivray, 1883) and *E. magna* (MacGillivray, 1895) (see below). Duvergier (1924: 18) had introduced *Exechonella* with the type species, *Cyclicopora? grandis* Duvergier (1921: 124, pl. 3, figs 2,3), originally recorded from the Lower Miocene (Aquitanian) of the Gironde, France. Cheetham (1966: 62) noted that this was the type species by monotypy. He emphasised that the type species of *Exechonella* was not *Hiantopora magna* MacGillivray as stated by Canu & Bassler (1927: 4) and by Harmer (1957: 652). Cheetham commented "However irregular, Duvergier's introduction has priority". In addition, the selection by Vigncaux (1949) of "*C. grandis* Duvergier" as type species of his genus *Hippexechonella* means that the name is a junior objective synonym of *Exechonella*.

Several other genera have been assigned to the Exechonellidae, but all require a more complete examination of the morphology of their type, and any other relevant species, before their relationships can be established. They include *Anexechona* Osburn, for *A. ancorata* Osburn (1950: 96, pl. 11, fig. 1), from the Gulf of California. *A. ancorata* has large, vicarious avicularia, and the frontal shield has large pores. Colonies are encrusting and occasionally erect and adeoniform; ovicells and spines are lacking. Osburn described the ontogeny of the frontal shield as being similar to that of *Exechonella*. *Auarthropora* Smitt, 1868 (type species *Lepralia monodon* Busk, 1860) and *Tripopula* Canu & Bassler, 1927 (type species *Escharipora stellata* Smitt, 1873) also have frontal shields with foramina and surrounding calcification similar to that in *Exechonella*; the structure of the orifice and peristome is similar in these three genera. *Xynexecha* Gordon & d'Hondt, for *X. pulchra* Gordon & d'Hondt (1997: 15, figs 8,9), from New Caledonia superficially resembles *Exechonella marginata* (see

below), and has erect, cylindrical colonies, zooids with long, tubular peristomes, and a frontal shield with a restricted central area of foramina. However, this area is described as umbonuloid, but surrounded by a "cryptocyst" with "areolae". If this means a cryptocystal (lepralioid) frontal shield, with marginal frontal septular pores, it is quite unlike that of *Exechonella*. Alternatively, it is difficult to understand how a cryptocyst (which is an interior wall growing into a pre-existent coelom), can have marginal frontal septular pores, and give rise to an umbonuloid shield. The calcification of the long, tubular peristome is described as similar to that of the "cryptocyst", but whether it is inferred to be umbonuloid or lepralioid, and the nature of its coelomic relationships, are uncertain. Although obviously not closely related, the shield resembles that of an arachnopusiid genus, *Briaraehmia*, described by Gordon (1984). It seems probable that, in spite of its appearance, *X. pilehra* may not be referable to the Exechonellidae. The genus *Stephanopora* Kirkpatrick (1888) was referred to the Exechonellidae by Hayward (1988), who redescribed the type species, *S. cribrispinata* (Kirkpatrick, 1888) from Mauritius. Gordon (1993) expanded analysis of its morphology and added notes on *S. perelegans* (Harmer, 1957) from Indonesia. The complexity of the frontal spinose extensions of the umbonuloid shield obscures the similarities of these species to those of *Exechonella*, and is discussed below (p. 00). Hayward (1988) also provisionally referred *Anarthropora horrida* Kirkpatrick (1888) to *Exechonella*. *A. horrida* has zooids with an umbonuloid frontal shield, long tubular peristomes, and sporadic, pedunculate avicularia. Although it appears to be generically distinct from *Exechonella*, it certainly shares many characteristics with other Exechonellidae.

In contrast, the genus *Coleopora* sensu stricto has little in common with *Exechonella*. *Coleopora* was introduced by Canu & Bassler (1927, pl. 1, fig. 7) for a single "Recent" species, *C. verrucosa*. Later, Canu & Bassler (1929: 267, pl. 20, fig. 4, pl. 26, fig. 9) redescribed the same specimen (from Jolo in the Philippines, "Albatross" Station 5137). *Coleopora* was defined with a hyperstomial ovicell "never closed by the operculum", and figured with a zooidal frontal "punctured by small very numerous tremopores". Among these were thickened tubes, which were retouched in the illustrations, but appear to be hollow, and vary in number from 3-9 per zooid. Although no ovicell was figured, it was stated that the species was "in reproduction", and that the ovicell was "globu-

lar". Large foramina with a border, or raised edges, as in *Exechonella antillea* (Osburn, 1927) and *E. tuberculata* respectively, did not occur. *Coleopora* was assigned to the family Petraliidae. Harmer (1957: 897, pl. 54, figs 11, 12), however, considered it to be a synonym of the Pleistocene Italian genus *Teuchopora*, and assigned specimens of his "*T.*" *verrucosa* from New Guinea to the Teuchoporidae. He described the zooids with numerous small frontal pores and hollow papillae. Poluzzi (1977) redefined *Teuchopora* from type specimens and demonstrated in detail its distinction from *Coleopora*, as noted by Winston & Heimberg (1986: 15). Harmer (1957: 897) was uncertain of the affinities of his specimens and noted similarities with *Exechonella*. Winston & Heimberg (1986: 15, figs 33-34) described *Coleopora verrucosa* from Bali, and referred the genus to Exechonellidae. Their figures show zooid frontal shields with numerous, slit-like pores, interspersed with 3-4 scattered "hollow papillae". There is a marked contrast between their figures of *C. verrucosa* and those of *Exechonella brasiliensis* Canu & Bassler, 1928 (Winston & Heimberg, 1986: 15, figs 26, 27), which show large foramina with curved rims. Winston & Heimberg (1986: 16) noted that the species included in *Coleopora* may not be a monophyletic group. Very few of these, including the type species, seem to be referable to the Exechonellidae. For example, *C. gigantea* Canu & Bassler (1923), redescribed by Osburn (1952), from the Pleistocene and Recent of California respectively, and *C. seriata* Canu & Bassler, 1929, from the Philippines, also described by Hayward (1988) from Mauritius, have large, prominent imperforate ovicells and numerous small frontal pores. However, *C. erinacea* Canu & Bassler (1929: 268, pl. 19, figs 5-8), has figures which are heavily retouched, and may refer to more than one species, but appears to be referable to *Exechonella* (see p. 00). Very similar species of *Exechonella* occurred in North America in the Middle Eocene, and were described and figured by Canu & Bassler (1920), who originally referred them to other genera, but reassigned them later (Canu & Bassler 1929).

The stratigraphically earliest species of the family appears to be *Cheilopora? orbifera* Canu & Bassler (1920: 526, pl. 14, fig. 16) from the Claibornian (Middle Eocene) of the USA, together with *Cyelicopora laticeila* Canu & Bassler (1920: 427, pl. 55, fig. 6) and *Cheilopora preluccidoides* Canu & Bassler (1920: 527, pl. 68, figs 1, 2) both from the Jacksonian (Late Eocene). Cheetham (1966) recorded an almost contemporaneous, unnamed Eocene form from the

Bartonian of the Upper Bracklesham beds of southern England. Names of other Tertiary species from France and Italy were given by Canu & Bassler (1929) and Cook (1985). More than 15 nominal species of *Exechonella* have been described, and there are more than 50 records of variously named and unnamed taxa.

Records of several nominal Recent species are virtually pantropical to subtropical in distribution, which suggests that they may each include more than one taxon. One problem is that relatively few distinctive characters are available for comparison among specimens. There is a wide range in variation of character states among the records from different localities, but an almost equally wide range occurs within populations from neighbouring localities. Harmer (1957), Cook (1985) and Fransen (1986) have all commented on this variability, and the consequent difficulty which exists in distinguishing taxa. Australian records of specimens referable to *Exechonella* fall very approximately, into four groups of species, each with similar morphologies. The first group is large and includes the type species, *E. grandis*, and other Tertiary European taxa, the world-wide *E. antillea*-complex, *E. brasiliensis* and the three Eocene forms from North America mentioned above. It is represented in Australia by a Recent species, *E. papillata* sp. nov. from the Great Australian Bight. The second group includes the *E. magna*-complex, which has an almost entirely Australian Tertiary and Recent distribution, but does include some records from the Philippines. The third group includes Australian and other records of Recent *E. tuberculata*, *E. discoidea* and *E. ampillacca*. The fourth group consists entirely of the Australian Tertiary *E. marginata*-complex. The Australian fauna therefore includes records of two Tertiary, and four Recent species or species-complexes.

MORPHOLOGY

There are relatively few diagnostic characters available for discrimination of species in *Exechonella*. In spite of this, *Exechonella* is an "easily recognised" genus. The colonies are usually encrusting, and unilaminar. Overgrowths may occur, as in the multilaminar *Exechonella papillata*, some bilaminar specimens of *E. magna* (which also includes a single lunulitiiform colony), and the erect, quadrilateral branches of the *E. marginata*-complex. The very large zooids may be distinguished with the naked eye, those of *E. papillata*, *E. marginata* and *E. antillea* usually exceeding 1.0 mm in length, and reaching 1.6 mm in

E. gigantea Cook (1967: 339, pl. 2C, D) from west Africa. The ancestrulae are usually very small, but resemble later-budded zooids (Fransen 1986). Zooids are often budded singly, with little tendency to form part of a "growing edge" (see Cook 1985: 45), although a form of marginal growing zone does occur in *E. papillata* and *E. magna*.

The lateral septular pores of nearly all species are numerous and uniporous in all zooids which are deep vertically, like those of *E. cf. discoidea* and *E. papillata*, but are reduced to three series or less, in shallower zooids, such as those of *E. tuberculata* and *E. marginata*. The marginal septular pores provide communication between the visceral and hypostegal coeloms, and in most species remain visible throughout ontogeny, as in *E. magna*, where they may be prominent. They occur peripherally, and often distally to the peristome in a single series, but may also form groups at the proximal end, or in the lateral "corners" of zooids, as in *E. papillata* and *E. marginata*. In some species, with partially isolated, flask-like zooids, like *E. cf. discoidea*, they are extremely small, and occur close to the base of the exposed lateral faces of the zooids.

The frontal shield has umbonuloid ontogeny, which has been discussed in detail by Cheetham & Cook (1983) and Gordon (1993). Essentially, it consists of a fold of cuticle derived from the frontal marginal septular pores, growing above a pre-existing frontal membrane with contiguous operculum and fully developed and functional parietal muscles (Cook 1985). The basal-facing calcified surface of the fold is an exterior wall, and has an outer closely apposed cuticular surface. The upper-facing calcified surface of the frontal is an interior wall, with an overlying hypostegal coelom derived from marginal septular pores, beneath an investing cuticle.

The primary orifice is uncalcified and the early ontogeny of the calcified orifice resembles that of many "eribrimorphs" (Cook 1967), with an orificial bar, or even a peristome calcifying above the operculum before the rest of the shield is complete (Cook 1967, Gordon 1984). The resulting early calcified orifice is often a simple, almost circular structure; but in several species, an inner lamina on the distal side terminates laterally at the base of the peristome. This may be the "lining" mentioned by Harmer (1957: 655). The lateral ends of the lamina may appear as distinct, paired "condyles" (see Fransen 1986, fig. 29a, b) (Fig. 1B), or as "pockets" within the calcification (Fig. 3D). In species with long, tubular peristomes these are not usually observable. Orifices may vary markedly

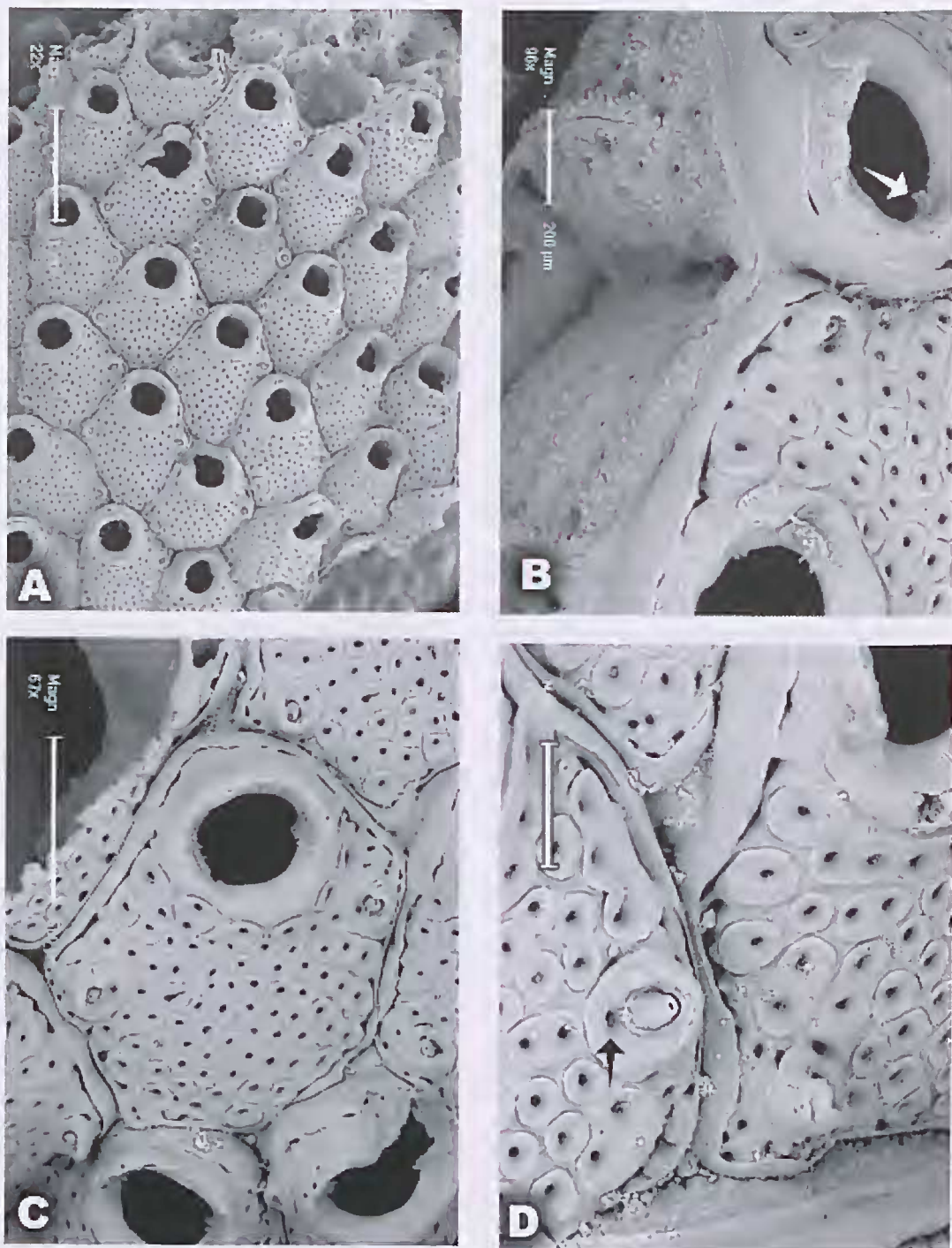


Fig. 1. A-D, *Exechonella papillata* sp. nov., NMV F97951, holotype, GAB Station 110. A. Zooids showing frontal shield with numerous foramina, calcified orifice with thickened peristome. Note raised zooid margins and lateral kenozooids, x17. B. Lateral vertical walls showing numerous uniporous septular pores, and frontal shield with thickened foraminal margins. Note small foramen associated with lateral kenozooid. Arrow points to edge of lamina in orifice, x67. C. Detail of zooid with distal lamina in orifice, two kenozooids. Note relation between marginal communication pores and zooid margin, x48. D. Detail of papillate kenozooid on left-hand zooid. Arrow points to adjacent foramen, x72.

within nominal taxa. For example, the orifices of *E. antillea* figured by Hayward (1974, Fig. 4C) from Chios, and by Winston (1982, fig. 60) from Florida, are far narrower proximally to the "condyles" than the orifices of *E. antillea* illustrated by Fransen (1986, fig. 29a, b), from the type region of Curaçao, and from Ghana by Cook (1985, pl. 15, A, B). In addition, "condyles" are absent in most colonies of Recent *E. magna*, but present in one Miocene population, at least, of the same nominal species. Peristomes may be raised, with irregular spinous projections on their margin, or be tubular and prominent, sometimes flaring outward terminally. Calcification is smooth on the inner surface, which is directly derived from the lower face of the calcified shield, and is part of the exterior wall. It is granular on the outer surface, which is an extension of the upper surface of the shield and is an interior wall, capable of developing secondary calcification.

The frontal shield develops a variable number of foramina in the calcification. Foramina are smaller, but have essentially the same calcified structure and relationships as peristomes. They may be distributed all over the frontal shield or be confined to an area of variable extent in the centre. They develop from uncalcified embayments among lobes of peripheral calcification, and are cut off and isolated as the lobes fuse progressively towards the centre of the shield (Fig. 2C). In some species, the cuticle is inserted at the edge of the foramina (e.g. in *E. magna*); in others, it is continuous across the face of the foramina (see Cook 1985: 46). The calcification surrounding the foramina is usually thin and smooth, but varies considerably among species and at different ontogenetic stages. Usually the edges of the foramina are thin and slightly upturned early in ontogeny. As the upper surface of the shield thickens, the foramina deepen and become surrounded by a rim of calcification. If the outer edges of the rim are thicker than the inner edges, the foramina appear as pits in the centre of a smooth disc of calcification. Where the foramina are scattered, the subsequent appearance is similar to that illustrated in *E. antillea* from the Gulf of California (Osburn 1950, pl. 10, fig. 9). If the foramina are more numerous, the edges of the discs abut, but do not fuse, resulting in an appearance like that figured in *E. antillea* from Chios (Hayward 1974, fig. 4C), in *E. antillea* from Ghana (Cook 1985, pl. 15B and fig. 38), in *E. preluccidioides* from the Eocene of South Carolina (Canu Bassler, 1920, pl. 68, fig. 1), in Miocene *E. marginata* from Muddy Creek, Victoria (Fig. 6D), and Recent *Exechonella papillata* sp. nov. from southern

Australia (Fig. 1B). If the foramina are infrequent, and their rims are curved, their appearance resembles that figured for *E. brasiliensis* from Brazil (Canu & Bassler 1928 pl. 3, fig. 5), from Komodo Island (Winston & Heimberg 1986, figs 26, 27), and from Vanuatu (Tilbrook *et al* 2001, fig. 8G). If the foramina are more numerous, their rims abut, and appear similar to those figured in *E. antillea* from Jamaica (Winston 1982, fig. 60), and *E. orbifera* (Canu & Bassler 1920, pl. 14, fig. 16) and *E. laicella* (Canu & Bassler 1920, pl. 55, fig. 6) from the Eocene of Alabama and North Carolina respectively. Although the foramina of species such as *E. papillata* sp. nov. and *E. cf. discoidea* appear to be open on the basal, exterior wall surface, it is inferred that the cuticular layer which lines the wall, is complete. The cuticle investing the hypostegal coelom inserts sporadically on the outer edge of each foramen, and is raised above it in life. Preserved specimens show a cuticular layer covering the foraminal opening, and often in dried material, shrinking into the upper part of the foramen (Fig. 4C), as observed in *E. antillea* by Cook (1985: 46). This type of foramen appears to occur in Group 1 and Group 3 species, but not in *E. magna* (Group 2), where the foramina are completely open (Fig. 2B). A thin intervening coelom is presumed to surround the edges of the foramina and to remain in contact with the visceral coelom through the frontal marginal septular pores. Sometimes a cuticular trace surrounds a group of foramina, often giving a superficial appearance of a costate shield (Fig. 1B, and Cook 1985, pl. 15B). There is no simple correlation between form and frequency of the foramina and the number and position of septular pores. A single, very prominent, marginal series is present in several populations of *E. magna*, but the foramina do not develop much further, after the initial ontogenetic stages, and the calcification around them is smooth and not greatly thickened. In contrast, in *E. tuberculata*, the pores are fewer and obscured, but the foramina are marginally raised in irregular spinous processes, and the intervening calcification is thick and granular.

Opercula with marginal sclerites have been reported in *E. antillea* by Cook (1985), and Fransen (1986), and are present in *Exechonella papillata* sp. nov. and some, but not all populations of *E. magna* from southern Australia (see below). Fransen (1986) considered that the opercula were attached to the condyles, but Cook (1967), who observed living specimens of the same nominal species, noted that they were closely apposed to the calcified orifice, but were drawn downwards, together with the frontal mem-

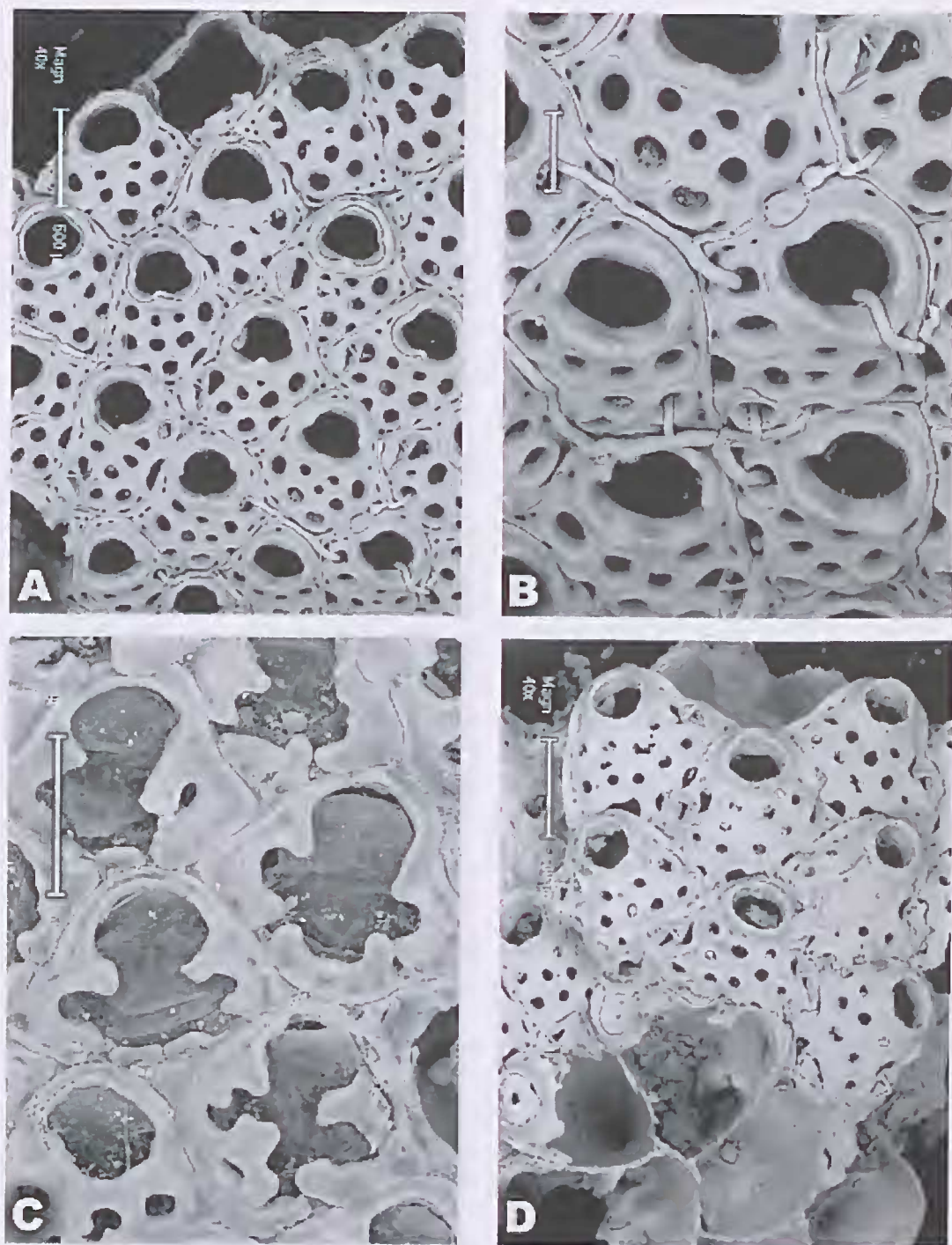


Fig. 2. A-D, *Exechonella magna* (MacGillivray 1895). A, B, GAB Station 103. A, Zooids with orifices showing proximal peristomial processes, avicularia with associated foramina, x28. B, Detail showing tubes of commensal organisms. Avicularia at top right and bottom centre, x57. C, GAB Station 134. Colony air-dried to show frontal membrane and operculum beneath incompletely calcified frontal shield, x47. D, Miocene, Muddy Creek. Central zooid with two avicularia, x28.

brane, almost to the basal wall, before opening, and protrusion of the tentacle sheath and crown (Cook 1985).

Small avicularia are frequently, but not invariably present. They are derived from a lateral, often oral, marginal frontal septular pore. Mandibles are slung on a delicate bar, and their shape is usually specifically correlated. Avicularia are generally very similar in material of each nominal species, but they are frequently absent from entire colonies, or parts of colonies. In the *E. magna*-complex, each avicularium is closely associated with a foramen, which may be larger than those occurring elsewhere in the shield. Structures which are not avicularia, but which have similar relationships with a foramen, occur in *Exechonella papillata* sp. nov. (see below).

Spines and ovicells are absent. Apart from the very doubtful and unillustrated record of ovicells in *E. discoidea* Canu & Bassler (1929, see below), they have not been reported in *Exechonella*. Cook (1985) described some enlarged, dimorphic, zooids in one specimen from west Africa referred to *E. antillea*. Fransen (1986) has illustrated the interior ovisac and brooding of embryos in non-dimorphic zooids of *E. antillea* sensu stricto.

NOTES ON AUSTRALIAN SPECIES OF *EXECHONELLA*

Exechonella Duvergier, 1924

Type species. Cylicopora? grandis Duvergier, 1921.

Group 1. *Exechonella papillata* sp. nov. (Figs 1A-D)

Holotype. NMV F97951 (figured specimen). Great Australian Bight. GAB Station 110, south of Esperance, Lat. 34°32' S, Long. 121°32' E, 154 m.

Paratype. NMV F97952 as above, large, multilaminar colony, originally encrusting shells, totalling 2500 zooids.

Other material. NMV GAB Station 089, southeast of Esperance, WA, Lat. 34°37' S, Long. 123°32' E, 210 m., single colony encrusting cemented sand, about 100 zooids.

Etymology. *papilla* (L), a nipple, referring to the small kenozooids.

Diagnosis. *Exechonella* with low peristomes and numerous frontal foramina; zooids each with one or two lateral kenozooids associated with a small foramen.

Description. Colony encrusting, unilaminar to multilaminar, with overgrowths in random directions. Zooids large, defined by a raised laminar border surrounding a series of small, marginal frontal septular pores. Lateral interzooidal communication by numerous pores scattered over the entire vertical walls. In a few zooids, a pair of small multiporous pore-plates also occur near the frontal edge of the walls, particularly, but not exclusively, on the distal walls. Their position is not correlated with that of the kenozooids (see below). Calcified orifice subrounded, tending to angular at proximal margin, length and width subequal; with a sharply delineated, smooth, slightly thickened peristomial rim. Opereulum closely apposed to orifice, with well-marked lateral sclerites. A pair of "condyles" within the calcified orifice are apparently associated with a distal lamina lining the peristome (see Fig. 1B). Each zooid has up to 80 small, rounded frontal foramina, surrounded by a disc of smooth calcification. In one or both lateral "corners" of many zooids, a small, round, kenozooidal structure is derived from a septular pore. It is not an avicularium, but is slightly raised, with an occluded, nipple-like region, which has a small central pore. Some of these structures have an oval, raised margin, which closely resembles an avicularian rostrum. However, none of these show any sign of a bar or a mandible. Nearly all these kenozooids have a small foramen within the raised rim of calcification, placed laterally to the central structure (Fig. 1D). Although very different in appearance, the relationship of the structure with the foramen is the same as in avicularia of *Exechonella magna* (see below).

Dimensions. Lz 0.45-0.59 mm, lz 0.43-0.50 mm, Lap (for secondary calcified orifice) 0.24-0.26 mm, lap 0.28-0.31 mm.

Remarks. This species does not appear to have been described before. It closely resembles some descriptions of specimens assigned to the "*E. antillea*"-complex, but differs completely in the much larger number of frontal foramina, and the occurrence of the small, lateral kenozooidal structures. The large colonies have allowed the investigation of the structure and ontogeny of the frontal shield in some detail.

Distribution. Known from the type and one other

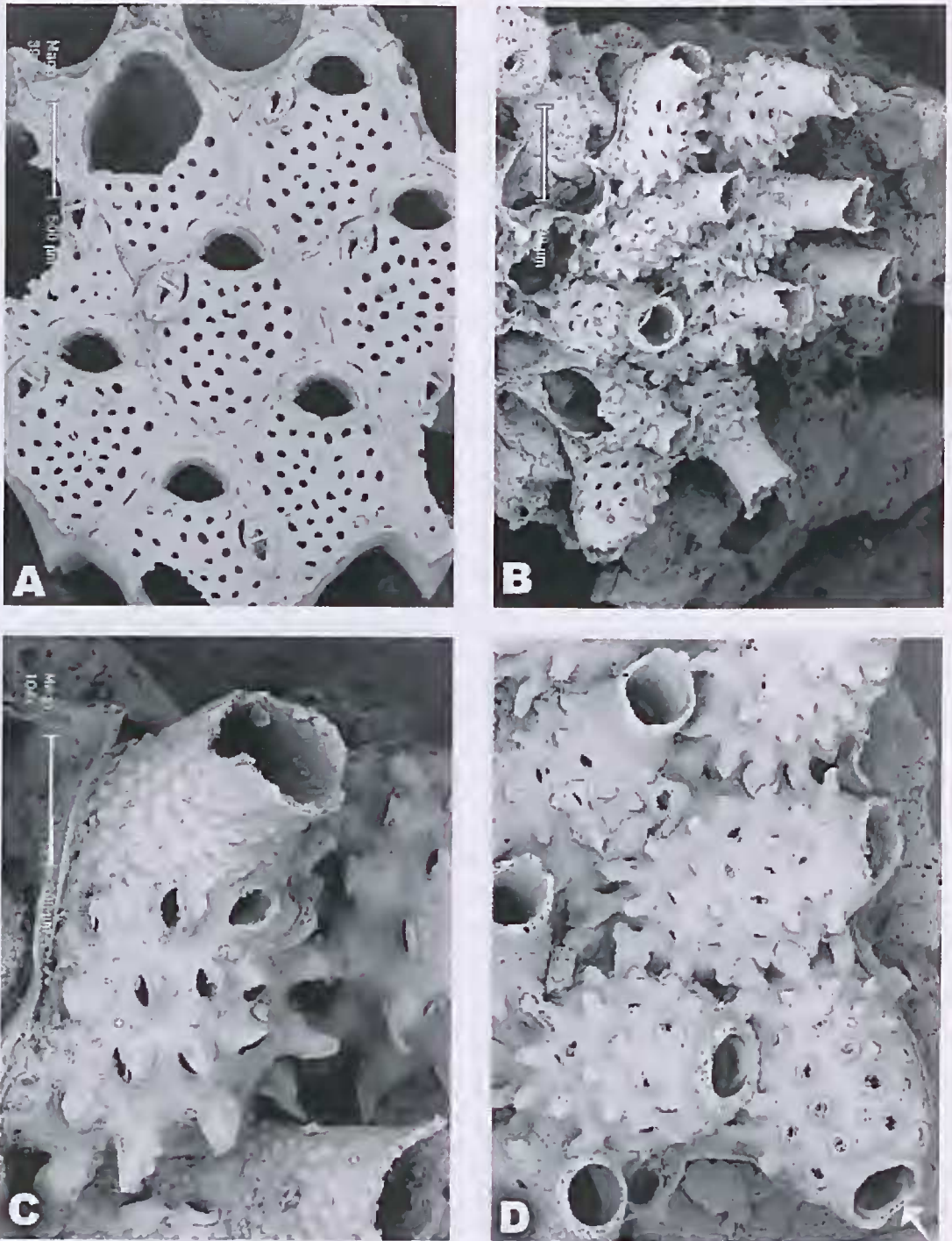


Fig. 3. A. *Exechonella magna* (MacGillivray 1895). Miocene, Balcombe Bay. Zooids with avicularia and about 30-40 small foramina, x29. B-D. *Exechonella tuberculata* (MacGillivray, 1883). Tangaroa 162. B. Small colony, showing tubular peristomes, and frontal foramina with raised, spinous marginal processes, x29. C. Single zooid, showing raised processes at edge of foramina, x95. D. Group of zooids. Note interzooidal fusion of some processes. Arrow shows "pockets" in orifice, x50.

locality, off southwestern Australia.

Group 2. *Exechonella magna* (MacGillivray 1895).
(Figs 2A-D, 3A)

Hiantopora magna MacGillivray 1895: 62, pl. 8, fig. 23, pl. 10, fig. 27.

Exechonella magna, Wass & Yoo 1983: 331, Fig. 1.
Exechonella paucipunctata Brown 1956: 600, Fig. 1.

Lectotype. NMV P27645, selected here, figured by MacGillivray 1895, pl. 8, fig. 2, Muddy Creek, Miocene, Victoria.

Paralectotype. NMV P27697, selected here, figured by MacGillivray 1895, pl. 10, fig. 27, Muddy Creek, Miocene, Victoria.

Other specimens. NMV. Miocene. Two encrusting, worn fragments, totalling 100 zooids, Muddy Creek, Victoria. Two unilaminar fragments totalling seven zooids, Bairnsdale, Victoria. Six bilaminar fragments, totalling 200 zooids, Balecombe Bay, Victoria

Recent specimens from the Great Australian Bight (see appendix p. 00 for details). GAB Station 054, young colony on adconid fragment, 16 zooids with growing edge and opercula. GAB Station 055, unilaminar fragment of 100 zooids. GAB Station 103, encrusting calcareous accretions with *Arachmopusia*, 200 zooids. GAB Station 105, young, ancestrulate colony encrusting massive "ecleporid" with other species, 60 zooids. GAB Station 114, large bilaminar colony fragment, approximately 2000 zooids. GAB Station 134, four specimens, two encrusting small shell fragments and one unilaminar piece, each with 200 zooids, with one, ancestrulate, free-living "lunulitiform" colony with no substratum or means of attachment, 50 zooids. GAB Station 139, two unilaminar fragments, totalling 1000 zooids. NMV 46836 (Marine Biology section), Port Phillip Heads, Victoria, three unilaminar fragments totalling approximately 160 zooids.

Description. Colonies usually encrusting, or with unilaminar expansions; zooids wide, lozenge-shaped, rather flat, outlined by a slightly raised border, with a variable number of small, frontal, marginal septular pores, which sometimes occur on the distal side of the calcified orifice. Calcified orifice rounded with straight to curved proximal margin, width greater than length; with a thin distal lamina, but generally with-

out "condyles", sometimes with raised proximal prominence. Operculum closely apposed to the calcified orifice; frontal membrane visible through the foramina. Frontal shield typically with from five to ten large, rounded foramina, but specimens with three, or up to 40 foramina known. Avicularia sporadic, lateral, acute, with a bar, flanked by a foramen, mandible elongated, orientated proximally.

Dimensions. Lz 0.75-0.96 mm, lz 0.64-0.78 mm, Lap (for secondary calcified orifice) 0.20-0.23 mm, lap 0.28-0.33 mm.

Remarks. Zooid size shows little variation within this species. However, other zooid characters such as number of foramina, varies considerably across populations, although within-colony variation is low. Zooids are defined by a shallow ridge and bordered by a series of small, marginal septular pores, which are sometimes numerous and well marked (Fig. 2A). Zooids are very deep, and communicate laterally by numerous uniporous septular pores. Unlike zooids of *Exechonella papillata* sp. nov., there seem to be no additional, multiporous pore plates. The calcified orifice is large, rounded, usually without "condyles", and slightly raised distally. In some material, there are small proximal or lateral processes on the edge of the shallow peristome, as in the specimen from GAB Station 103 (Fig. 2A). The colonies from GAB Station 134 exhibit a wide range of astogenetic and ontogenetic stages. One small, complete ancestrulate colony has no obvious substratum, and has developed a lunulitiform structure, with no apparent method of attachment. Another, virtually free-living, colony shows a number of zooids with partially calcified frontal shields (Fig. 2C). Although it appears probable that this is a reaction to a microenvironmental influence, it does show the essential stages in frontal shield development. The apposed opercula and visible frontal membranes are a prominent feature of this specimen. Intraspecific variation is most obvious in characters of the frontal shields. In the fossil type specimens the shields have a range of 12-16 somewhat worn and irregular frontal foramina, and worn avicularia are present in a very few zooids. The supplementary, encrusting specimens from Muddy Creek resemble the type fragments closely, although they have a lower number (8-12) of foramina. One zooid has two avicularia (Fig. 2D). This is a very rare occurrence, but a similar zooid was figured in a population referred to *E. magna* from the Philippines by Canu & Bassler (1929, pl. 19, figs 1-2). The number of fo-

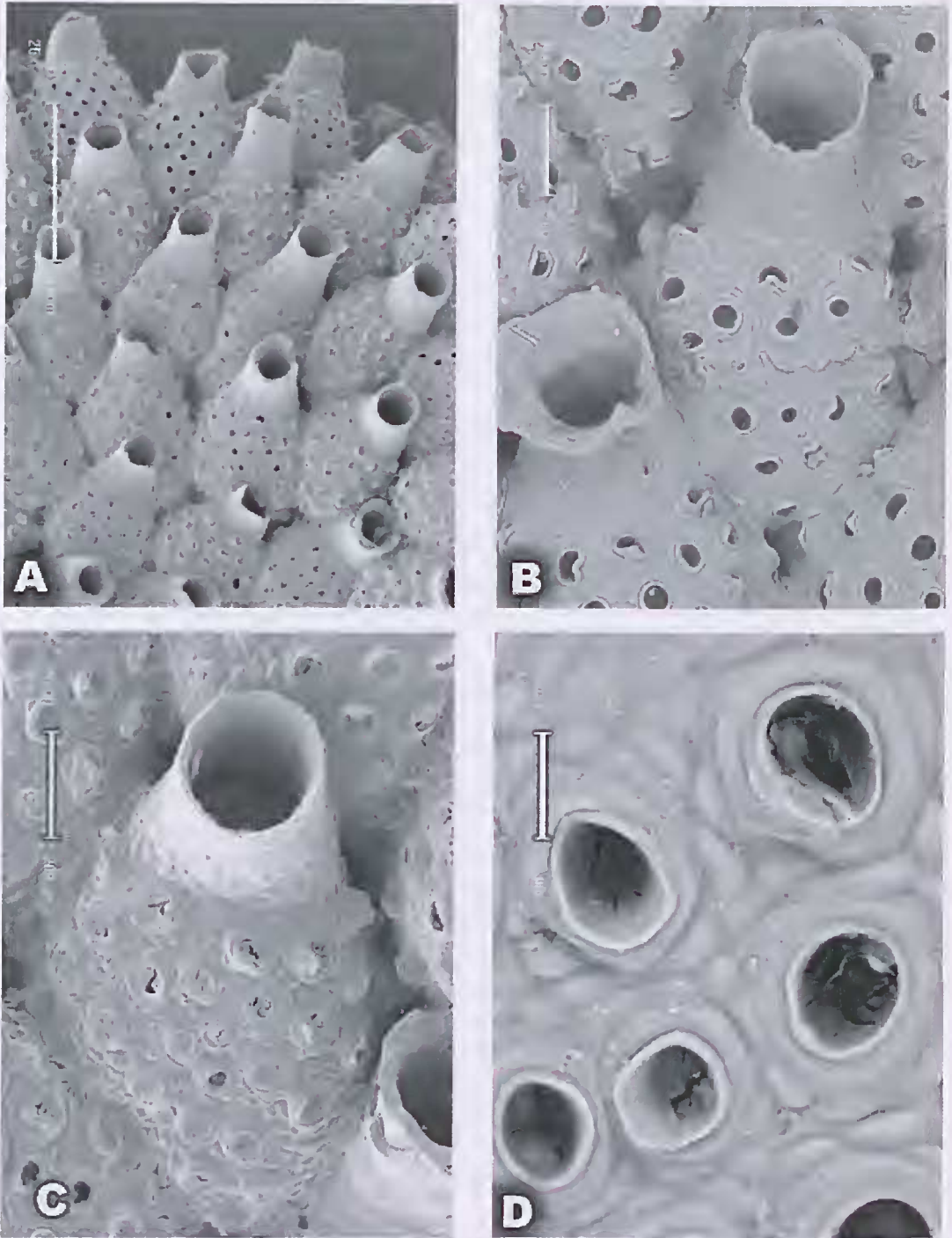


Fig. 4. A-D. *Exchionella* sp. cf. *discoidea* Canu & Bassler, 1929. GAB Station 119. A. Part of colony, air-dried, showing tubular peristomes, secondary electron image, x24. B. Detail of two zooid showing frontal calcification, back-scattered electron image, x65. C. Single zooid, secondary electron image to show cuticular cover of foramina, x78. D. Detail of foramina showing cuticular cover and calcified rim, back-scattered electron image, x310.

ramina in the unilaminar and encrusting specimens from Muddy Creek and Bairnsdale is in complete contrast to those in the zooids of the large, well preserved, bilaminar fossil specimens from Balcombe Bay. These have paired orificial "condyles" formed by a calcified lining within the distal rim of the orifice, which is wide and less rounded than those of other specimens. The frontal shields have from 28 to 40 rather small foramina, and the zooids present an appearance very different from that of the other fossil and Recent specimens (Fig. 3A). It is probable that if additional specimens became available, with these consistently different sets of characters, they could be regarded as specifically distinct from *E. magna* sensu stricto. The Recent specimens from the Great Australian Bight, figured by Wass & Yoo (1983: 331, fig. 11), have a lower range of five to nine frontal foramina, and resemble those from GAB Station 139. None of these zooids appears to have "condyles", but some have a slightly convex proximal edge to the peristome. The encrusting specimens from GAB Station 103, like the large, bilaminar colony from GAB Station 114, have an average of ten foramina, and avicularia are rare (Fig. 2A). Opercula are generally not markedly thickened with sclerites, or marginally flanged, as they are in some populations of the "*E. antillea*"-complex (Cook 1985, Fransen 1986). Thin marginal opercular sclerites are present in the young colony from GAB Station 105, but are not obvious in the large colony from GAB Station 114. The frontal foramina all have a slightly raised and thickened rim, and their shape is directly correlated with their frequency. The numerous foramina in the fossil specimens from Balcombe Bay are regularly rounded, whereas those from GAB Station 139 are infrequent and irregular in size and shape. Specimens from the Pliocene of South Australia, described and illustrated by Brown (1956: 600, fig. 1) as *E. paucipunctata*, appear to represent an end-term in the range of variation of frontal foramina in the *E. magna*-complex. The zooids had only three to four large, irregular foramina, but most other characters do not differ greatly from specimens examined here. The large foramina of *E. magna* are open, as is obvious from the occurrence of commensal organisms of unknown relationships, producing thin calcified tubes which wind in and out of the foramina (Fig. 2B). The specimen illustrated was alive when collected, and the cuticular frontal membrane and other uncalcified tissue was removed using bleach before examination by SEM. Although it is not known if any other species possesses similarly open foramina, this appears to be an

important distinction between *E. magna* and the other species described here. A slide in the Museum Victoria collection (old registration 46836) from Port Phillip Heads, presumably collected in the late 19th century, is similar to the material from the Great Australian Bight, especially GAB Station 103 (Fig. 2A,B).

Avicularia are similar in all specimens. They originate from a marginal septular pore and are small, elongated, and raised, orientated proximally, with a slightly hooked mandible slung on a bar. They are always flanked on the inner side by a foramen, which is often enlarged, but has the same relationships as the foramen bordering the kenozooid in *E. papillata* (see above).

Other records dubiously referred to *E. magna* are those of Canu & Bassler (1929: 121, pl. 19, figs 1-4) from shallow water in the southern Philippines, and of *Lepralia foraminigera* var. Kirkpatrick (1890: 16, 19), described briefly from the type specimen from the China Sea by Harmer (1957: 654, fig. 52). The material from the Philippines was encrusting, and had zooids with 10-15 foramina, prominent, thickened peristomes and paired avicularia. Harmer mentioned that the avicularian mandibles of Kirkpatrick's specimen were setiform and projected beyond the rostrum terminally. These two populations are therefore probably not conspecific with *E. magna* sensu stricto, although they are certainly very similar in several characteristics to the specimens described here, and with them form a species-complex which has been present in the Australian region from the Miocene to the Recent.

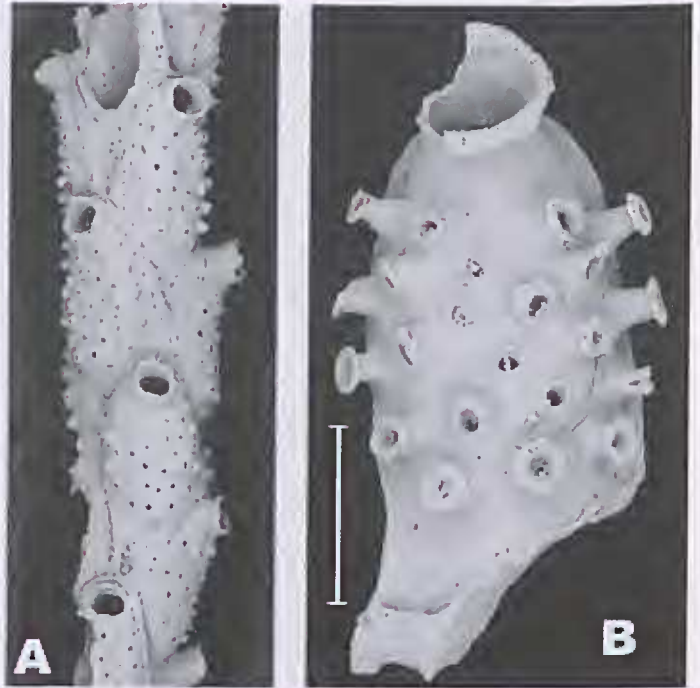
Group 3. *Exechonella tuberculata* (MacGillivray, 1883).
(Figs 3B-D)

Lagenipora tuberculata MacGillivray 1883: 132, pl. 3, fig. 15.— MacGillivray 1888: 209, pl. 156, figs 1, 2.

Material examined. Holotype, NMV F45627, MacGillivray collection, Port Phillip Heads, Victoria. Additional specimens from Bass Strait Survey, "Tangaroa" Station 162, three ancestrulate colonies on small shells with 15 other species, totalling 60 zooids; BSS "Tangaroa" Station 155, ancestrulate colony on shell with two other species, totalling 70 zooids.

Description. Colonies small and encrusting, with large

Fig. 5. A-B. *Exechonella marginata* (MacGillivray, 1895), Mioocene, Balcombe Bay. Part of an erect branch, showing zooids with raised peristomes and foramina, $\times 18$. B. Zooid showing raised peristome, long, tubular frontal foramina, and proximal septular pores, $\times 45$.



zooids, although those of the ancestrular region are small. Zooids communicate laterally through one or two series of very small pores. The peristomes are long and tubular, but are often semi-repent and not prominent. The calcified orifice has a distal lamina which forms a pair of pockets, resembling ocluser laminae, at the base of the peristome (Fig. 3D), but "condyles" seem to be absent. The frontal shield is prominent and swollen, obscuring a single series of minute marginal septular pores within the limits of a very shallow interzooidal lamina. The number of foramina is rarely more than 20. They are circular very early in ontogeny, but rapidly become partially obscured, and are raised, often unilaterally, to form long, irregular, spinous processes which may fuse with those of neighbouring frontal shields. There are no avicularia.

Dimensions. Lz about 0.95 mm (excluding peristome), lz about 0.63 mm.

Remarks. The type specimen resembles MacGillivray's figures (1883: 132, pl. 3, fig. 15 and 1888: 209, pl. 156, figs 1, 2) closely. Although there are many records of this species, from an extensive geographical range, there are few illustrations of *E. tuberculata*, other than those of MacGillivray. The

species has been reported from a wide range of localities extending from the Red Sea (Dumont 1981), through the Indian Ocean to the Philippines and East Indies (Harmer 1957), the specimens included here are those from the Port Phillip and Bass Strait area only. Although it is possible that they are conspecific with the other specimens described below (see *E. cf. discoidea*), they do differ in details of the calcified orifice and the development of frontal foramina.

Exechonella* sp. cf. *discoidea Canu & Bassler, 1929
(Figs 4A-D)

?*Exechonella discoidea* Canu & Bassler 1929: 123, pl. 20, figs 5, 6

?*Exechonella ampullacea* Hayward & Ryland 1995: 543, fig. 7E

?*Exechonella tuberculata* Gordon 1984: 70, Pl. 23D, not MacGillivray 1883, see above.

Material examined. Great Australian Bight, GAB Station 119, one colony, on other bryozoans, 50 zooids. GAB Station 065, two colonies, one ancestrulate colony, on shell, totalling 50 zooids. GAB Station 134, two small colonics encrusting large, calcareous ac-

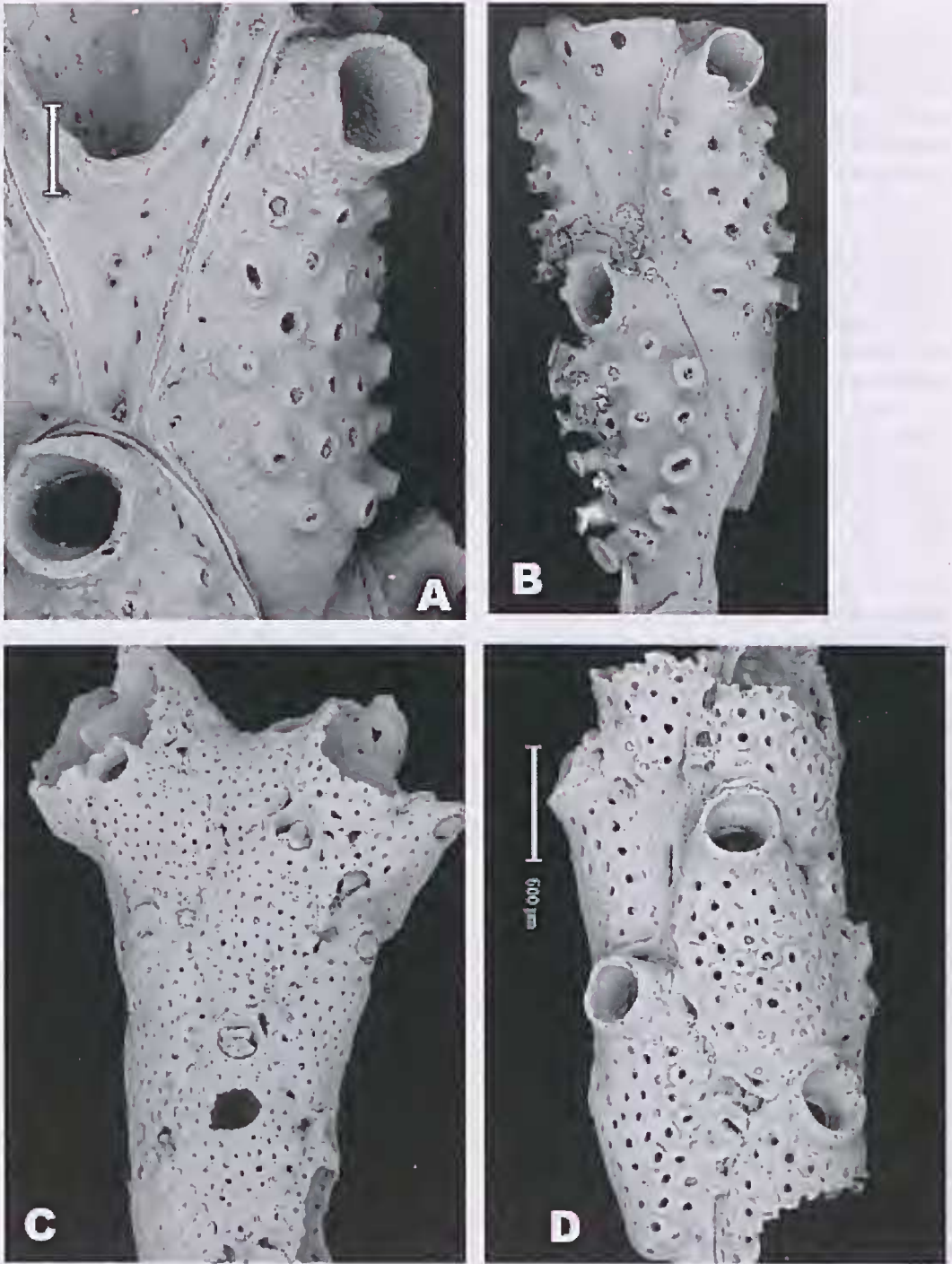


Fig. 6. A-D. *Exechonella marginata* (MacGillivray, 1895). A-B. Miocene, Balcombe Bay. A. Zooid showing tubular peristome and raised frontal foramina. Note the proximal grouping of frontal septular pores on zooid to left, x65. B. Group of three zooids showing long, tubular frontal foramina, x30. C-D. Miocene, Muddy Creek. C. Part of colony with branch bifurcation, x23. D. Detail of another colony, with zooids showing frontal calcification, and processes crossing zooids, x34.

cretion, totalling 50 zooids. GAB Station 139, colony on shell accretion, totalling 120 zooids.

Description. Colony encrusting, zooids small early in astogeny, later up to 1.3 mm in length, flask-shaped, with raised, tubular peristomes. Frontal foramina up to 25, slightly irregular and raised marginally. Calcified orifice apparently without distal lamina or "condyles", shallow, curved proximally. Marginal septular pores small, placed near the basal part of the lateral curvature of the frontal wall; no lamina apparent between zooids. Avicularia absent.

Remarks. The specimens, which are all from the western part of the Great Australian Bight, from 40-150 m depth, most resemble those reported by Gordon (1984) as *E. tuberculata*, from the Kermadec Ridge region, north of New Zealand, from 40-130 m depth. They have a similar flask-like shape, with long, tubular peristome, and a similar range in zooid length (approximately 0.9-1.4 mm), and number of frontal foramina (average 25).

The slightly irregularly-shaped foramina are raised marginally, and are surrounded by mamillate calcification, in contrast to the discs of smooth calcification surrounding the foramina in *E. papillata* sp. nov. In untreated specimens, the dried cuticle is seen stretched across the top of the raised foramen margin (Fig. 4C).

E. discoidea Canu & Bassler (1929) from Mindanao in the Philippines, from approximately 70 m depth, also shares some characteristics. The colonies were very small, and probably astogenetically young. The figured zooids are generally less than 1 mm in length. The zooids have long, somewhat irregular peristomes, and the number of foramina averages 15. The specimens named *E. tuberculata* from "Siboga" Station 164 (west end of New Guinea, 32 m), include two species, one of which has flask-like zooids less than 1 mm in length, with long tubular peristomes, and 15-19 foramina (see Harmer 1957, pl. 54, fig. 14). This appears to be very close to *E. discoidea*. Harmer (1957) also included another Philippine species, *Coleopora erinacea* Canu & Bassler (1929: 268, pl. 19, figs 6-8). This certainly belongs to *Exechonella* (see Harmer 1957: 653, footnote), not *Coleopora*. Some, but not all, of Canu & Bassler's illustrations (for example pl. 19, fig. 7), also appear to be close to *E. discoidea*, but without examination of further specimens, it is not possible to determine their identity. *E. discoidea* was originally described as having ovicells, but these were not illustrated. Another, somewhat similar species, *E. ampullacea*, with

raised, tubular peristomes, but smaller zooids (0.7-0.9 mm), with more numerous, rounded foramina (up to 40), was described from shallow water from the Great Barrier Reef by Hayward & Ryland (1995: 547, fig. 7E). It somewhat resembles both *E. discoidea* and the specimen from the Kermadec region illustrated as *E. inberculata* by Gordon (1984).

Group 4. *Exechonella marginata* (MacGillivray, 1895).
(Figs 5A, B, 6A-D)

Tubucellaria marginata MacGillivray 1895: 105, pl. 4, figs 2, 3.—Maplestone 1904: 214.

Type material. NMV P27553, figured by MacGillivray 1895, pl. 4, figs 2, 2a, 2b. Muddy Creek, Victoria (Population 1). NMV P 27554, figured by MacGillivray 1895, pl. 4, fig. 3, Schnapper Point, Victoria (Population 2).

Other material examined. Population 1. Muddy Creek, Victoria, nine quadriserial fragments, totalling 65 zooids. Grices Creek, Victoria, five fragments, totalling 55 zooids. Population 2. Balcombe Bay, Victoria, 15 fragments, totalling 65 zooids. Batesford Quarry, Victoria, 7 fragments totalling 17 complete zooids. Bairnsdale, Victoria, 5 fragments totalling 12 zooids. Population 3. Coorimungle, 10 fragments, totalling 25 zooids. Balcombe Bay, 11 fragments, totalling 37 zooids.

Description. Colony creet, branching; branches cylindrical, nearly all quadriserial, with one from Muddy Creek showing a dichotomous branch. Zooids elongated, defined by a raised rim of calcification, bordering a marginal series of septular pores. Laterally, the zooids communicate by one or two series of scattered pores. Calcified orifice almost circular, lacking "condyles", peristome often very raised and tubular, sometimes flaring terminally. Frontal shield includes a very variable number of rounded foramina, each with a raised rim. Avicularia absent.

Dimensions. Lz about 1.4 mm, lz about 0.68 mm. Lap (secondary orifice) about 0.26 mm, lap about 0.27 mm.

Remarks. MacGillivray (1895: 105) referred this species to the genus *Tubucellaria* d'Orbigny, 1852. It was listed by Maplestone (1904: 214) from several other Tertiary Victorian localities. MacGillivray's (1895) figures illustrate two of the populations exhibiting part

of the range of variation. In the Population 1 zooids illustrated in Figures 2, 2a and 2b, and the specimens from Muddy Creek and Grices Creek examined here, there are 50-60 closely spaced foramina with rounded, but not greatly raised margins. The hypostegal coelom appears to develop extrazoooidal lobes of calcification, which extend above the zooidal margins and septular pores, and fuse with lobes from neighbouring zooids, leaving a series of irregular embayments (Fig. 6C, D). This extrazoooidal calcification is present in all specimens examined, and, in fact, was illustrated by MacGillivray in Pl. 4, fig. 2a, at the proximal end of the fragment. Zooids from Population 2 were illustrated by MacGillivray in Pl. 4, fig. 3, from a specimen from Schnapper Point. Specimens from Bairnsdale, Batesford Quarry and Balcombe Bay resemble these figures in having more prominent peristomes, and zooids with from 30-40 frontal foramina, which are more widely spaced, and often raised marginally (Fig. 5A, 6A). The branch fragments and the zooids of Populations 1 and 2 are generally not as robust as those of Population 3 (Fig. 5B, 6B). The zooids from Coorimungle and Balcombe Bay, belonging to this population, are very large and defined by a distinctly raised rim. There is a series of marginal septular pores, which may be grouped in an extensive, depressed area of proximal frontal shield which has no foramina. The peristome is raised, tubular and often prominent. The most noticeable difference in these zooids is in the number of frontal foramina, which rarely exceed 24, and may be as low as 12. The foramina are confined to an area in the central part of the frontal shield, and the calcification surrounding them is smooth. Most foramina are raised and tubular, some equalling the peristome in length, and nearly all flaring terminally. There is no development of extrazoooidal bridges of calcification between zooids, as in the zooids of Population 1.

Although the specimens examined fall fairly clearly into three population groups, the form of the foraminal calcification is correlated with frequency, as it is in *E. magna*. Only investigation of much larger samples of each morphotype would show whether there were two or more distinct taxa present or not. The inner surface of the tubular foramina is part of the exterior wall forming the basal side of the shield, and has no connection with the visceral coelom. The area frontal to the upper, interior-walled part of the shield is inferred to have been occupied by hypostegal coelom bounded by cuticle, presumably carried up frontally and surrounding the tubular foramina. Although the foramina of *E. tuberculata* develop in a

somewhat similar way, they are not as extensive. Harmer (1957: 653) included *T. marginata* in the synonymy of *Exechonella tuberculata*. It differs in colony form, in the relationships of the marginal septular pores to the rest of the frontal shield, and in the form of the frontal foramina. It also differs in the absence of internal "pockets" at the base of the peristome.

Relationships. The development of a considerably more extensive secondary and tertiary frontal shield, derived from a hypostegal coelom, occurs in another genus which has been referred to the Exechonellidae. This is *Stephanopora* Kirkpatrick, described in detail by Hayward (1988) and by Gordon (1993). In *S. cribrispinata* Kirkpatrick, the tubular expansions of foramina are raised as in *E. marginata* Population 3, but fuse with each other terminally. They form a porous, secondary shield composed of exterior wall, derived from the lower surface of the umbonuloid primary shield. The hypostegal coelom remains to form a labyrinthine intervening layer at a lower level. Hollow spinous outgrowths from the peristome then fuse interzooidally, forming a tertiary shield. In another species of *Stephanopora*, *S. perelegans*, the flattened, "semi-spinous" processes derived from the peristome, have a structure exactly like that of an umbonuloid wall, namely, their basal side is exterior, but the frontal side is an interior wall covered by an extension of hypostegal coelom and bounded by a cuticle. This type of development is remarkably similar to that described in the Cretaceous archnoposiid genus *Ramicosticella* by Voigt & Gordon (1998). The type species, *R. erratica*, from the Danian of Germany, produces the equivalent of an umbonuloid shield from pairs of branched, flattened semi-spines which originate at the proximal end of the zooid, from paired septular pores, and spread interzooidally over the zooid frontals, fusing irregularly. Voigt & Gordon (1998) discounted this form of development as a possible indication of an origin of some umbonuloid walls, from "cribrilinid" costae which were uncalcified frontally. There is, admittedly, no earlier fossil evidence for a linking form or forms, but this type of origin remains feasible, as it requires no more than the control of calcification at specific sites, which is inherent in the Bryozoa in general, and is expressed in a random and mosaic manner. The different kinds and degrees of distribution and development of hypostegal coeloms in the Exechonellidae suggests that there were almost certainly more methods of producing frontal shields than have at present been established.

ACKNOWLEDGEMENTS

We should like to thank Dr. Yvonne Bone (University of Adelaide) and the Master and crew of C.S.I.R.O. MV "Franklin" for the opportunity for one of us (P.E.B.) to participate in the program which collected material from the Great Australian Bight in July 1995. Chris Rowley, Dr David Holloway, and Dr Rolf Schmidt have kindly made specimens from the Museum of Victoria collections. An earlier version of this paper was read at the 2001 Dublin Conference of the International Bryozoology Association.

APPENDIX

LOCALITIES MENTIONED IN THE TEXT

Tertiary of Victoria.

Bairnsdale. Approximately 12 km west of Bairnsdale. Lat. 37°47.9'S, Long. 147°29.5'E.

Age: Miocene.

Balcombe Bay and possibly Schnapper Point. On the coast of Port Phillip Bay,

approximately 3 km south of Mornington. Lat. 38°14.5'S, 145°01.7'E. Fyansford Clay. Age: Balcombian, Middle Miocene (Langhian).

Batesford Quarry. Upper levels of limestone quarry, 7 km west of Geelong. Lat. 38°06.5'S, Long. 144°17.3'E. Fyansford Clay. Age: Balcombian, Middle Miocene

(Langhian).

Caoriemungle. Road cuttings approximately 18 km north of Princetown. Lat. 38°32.4'S,

Long. 143°08.1'E. Gellibrand Marl. Age: Balcombian, Middle Miocene.

Grices Creek. On the coast of Port Phillip Bay, approximately 8 km north of Mornington. Lat. 38°11.9'S, Long. 145°03.9'E. Fyansford Clay. Age: Balcombian (some material may be Bairnsdalian), Middle Miocene.

Muddy Creek. Clifton Bank, Muddy Creek, 8 km west of Hamilton. Lat. 37°44.6'S, Long. 141°56.4'E. Muddy Creek Marl (=Gellibrand Marl). Age: Balcombian, Middle Miocene.

R.V. Franklin cruise, July 1995, Great Australian Bight stations.

GAB054: N. E. of Esperance. Lat. 33°12'S, Long. 124°55'E, 54 m.

GAB055: N. E. of Esperance. Lat. 33°16'S, Long. 125°18'E, 59.5 m.

GAB065: N. E. of Esperance. Lat. 33°03'S, Long.

124°23'E, 42.5 m.

GAB103: off Esperance. Lat. 33°58'S, Long. 121°56'E, 55 m.

GAB105: SW of Esperance. Lat. 34°04'S, Long. 121°44'E, 78 m.

GAB110: S. of Esperance. Lat. 34°32'S, Long. 121°32'E, 154 m.

GAB114: SW of Esperance. Lat. 34°37'S, Long. 121°32'E, 190 m.

GAB119: E of Albany. Lat. 35°S, Long. 119°E, 149 m.

GAB134: W of Cape Mentelle. Lat. 34°02'S, Long. 114°48'E, 51 m.

GAB139: W of Cape Naturaliste. Lat. 33°35'S, Long. 114°46'E, 49 m.

NMV Bass Strait Survey stations.

Tangaroa (BSS) 155: Lat. 38°34'S, Long. 144°54.3'E, 70 m

Tangaroa (BSS) 162: Lat. 39°46'S, Long. 146°18'E, 80 m.

REFERENCES

- BROWN, D. A., 1956. Some Pliocene Polyzoa from South Australia. *Annals and Magazine of Natural History* (12) 9: 593-611.
- BUSK, G., 1860. Zoophytology. Shetland Polyzoa. Collected by Mr. Barlee (Continued and concluded). *Quarterly journal of microscopical science* 8: 213-214.
- CANU, F. & BASSLER, R. S., 1920. North American Tertiary Bryozoa. *Bulletin of the United States National Museum* 106: i-xx, 1-879.
- CANU, F. & BASSLER, R. S., 1923. North American later Tertiary and Quaternary Bryozoa. *United States National Museum Bulletin* 125: 1-302.
- CANU, F. & BASSLER, R. S., 1927. Classification of the cheilostomatous Bryozoa. *Proceedings of the U.S. National Museum* 69: 1-42.
- CANU, F. & BASSLER, R. S., 1928. Bryozoaires du Brésil. *Bulletin de la Société des Sciences de Seine-et-Oise* 9 (5): 58-100.
- CANU, F. & BASSLER, R. S., 1929. Bryozoa of the Philippine Region. *Bulletin of the United States National Museum* 100: v-ix, 1-685.
- CHEETHAM, A. H., 1966. Cheilostomatous Polyzoa from the Upper Bracklesham Beds (Eocene) of Sussex. *Bulletin of the British Museum (Natural History) Geology* 13 (1): 1-115.
- CHEETHAM, A. H. & COOK, P. L., 1983. General Features of the Class Gymnolaemata. In *Treatise on Invertebrate Paleontology, Part G, Bryozoa*

- Revised, Boardman, R. S. et al., eds, The Geological Society of America, Inc. and the University of Kansas, Boulder, Colorado and Lawrence, Kansas, 138-207
- COOK, P. L., 1967. Polyzoa (Bryozoa) from West Africa. The Pseudostega, the Cribrimorpha and some Ascophora Imperfecta. *Bulletin of the British Museum (Natural History) Zoology* 15 (7): 321-351.
- COOK, P. L., 1985. Bryozoa from Ghana, a preliminary survey. *Annales des Musées Royaux de l'Afrique Centrale, Tervuren, Belgique, sciences zoologiques* 238: 1-315.
- DUMONT, J. P. C., 1981. A report on the cheilostome Bryozoa of the Sudanese Red Sea. *Journal of natural history* 15: 623-637.
- DUVERGIER, J., 1921. Note sur les Bryozoaires du Néogène de l'Aquitaine. *Actes de la Société linnéenne de Bordeaux* 72: 145-181.
- DUVERGIER, J., 1924. Deuxième note sur les Bryozoaires du Néogène de l'Aquitaine. *Actes de la Société linnéenne de Bordeaux* 75: 145-190.
- FRANSEN, C. H. J. M., 1986. Caribbean Bryozoa: Anasca and Ascophora Imperfecta of the inner bays of Curaçao and Bonaire. *Studies on the Fauna of Curaçao and other Caribbean Islands* 68: 3-119.
- GORDON, D. P., 1984. The marine Fauna of New Zealand: Bryozoa: Gymnolaemata from the Kermadec Ridge. *Memoirs. New Zealand Oceanographic Institute* 91: 1-198.
- GORDON, D. P., 1993. Bryozoan frontal shields: studies on umbonulomorphs and impacts on elasmification. *Zoologica Scripta* 22 (2): 203-231.
- GORDON, D. P. & D'HONDT, J.-L., 1997. Bryozoa: Lepraliomorpha and other Ascophorina from New Caledonian waters. *Mémoires du Muséum National d'Histoire Naturelle* 176, 9-124.
- HARMER, S. F., 1957. The Polyzoa of the Siboga Expedition. Part 4. Cheilostomata Ascophora II. *Siboga-Expeditie* 28d: v-xv, 641-1147.
- HAYWARD, P. J., 1974. Studies on the cheilostome bryozoan fauna of the Aegean Island of Chios. *Journal of Natural History* 8: 369-402.
- HAYWARD, P. J., 1988. Mauritian cheilostome Bryozoa. *Journal of Zoology. London* 215: 269-356.
- HAYWARD, P. J. & RYLAND, J. S., 1995. Bryozoa from Heron Island, Great Barrier Reef. 2. *Memoirs of the Queensland Museum* 38 (2): 533-573.
- KIRKPATRICK, R., 1888. Polyzoa of Mauritius. *Annals and Magazine of Natural History* (6) 1, 72-85.
- KIRKPATRICK, R., 1890. Report on the Hydrozoa and Polyzoa collected by P.W.Bassett-Smith, Esq., Surgeon R.N., during the survey of the Tizard and Macclesfield Banks, in the China Sea, by H.M.S. 'Rambler', Commander W.U.Moore. *Annals and Magazine of Natural History* (6) 5: 11-24.
- MACGILLIVRAY, P. H., 1883. Descriptions of New, or Little Known, Polyzoa. Part II. *Transactions and Proceedings of the Royal Society of Victoria* 19: 130-138.
- MACGILLIVRAY, P. H., 1888. Polyzoa. In *Prodrromus of the Zoology of Victoria, Decade XVI*, F. McCoy ed., Government Printer, Melbourne, 209-220.
- MACGILLIVRAY, P. H., 1895. A monograph of the Tertiary Polyzoa of Victoria. *Transactions of the Royal Society of Victoria* n.s. 4: 1-166.
- MAPLESTONE, C. M., 1904. Tabulated list of the fossil cheilostomatous Polyzoa in the Victorian Tertiary deposits. *Proceedings of the Royal Society of Victoria* n.s. 17: 182-219.
- D'ORBIGNY, A., 1852. *Paléontologie française, Terrains Crétacés, V. Bryozoaires*. Victor Masson: Paris: 185bis-472.
- OSBURN, R. C., 1927. The Bryozoa of Curaçao. *Bijdragen tot de Dierkunde, Amsterdam* 25: 123-132.
- OSBURN, R. C., 1950. Bryozoa of the Pacific coast of America, Part 1. Cheilostomata - Anasca. *Report of the Allan Hancock Pacific Expeditions* 14 (1): 1-269.
- OSBURN, R. C., 1952. Bryozoa of the Pacific coast of America, part 2, Cheilostomata-Ascophora. *Report of the Allan Hancock Pacific Expeditions* 14: 271-611.
- POLUZZI, A., 1977. Contributi per una revisione del genera *Tenchopora* Neviani 1895 (Bryozoa, Cheilostomata). *Bollettino della Società Paleontologica Italiana* 16: 69-77.
- SMITT, F. A., 1868. Kritisk förteckning öfver Skandinaviens Hafs-Bryozoen. IV. *Öfversigt af Kongliga Vetenskaps-Akademiens Förhandlingar* 25: 3-230.
- SMITT, F. A., 1873. Floridan Bryozoa collected by Count L.F. de Pourtales, Part 2. *Kongliga Svenska Vetenskaps-Akademiens Handlingar* 11: 1-83.
- TILBROOK, K. J., HAYWARD, P. J. & GORDON, D. P., 2001. Cheilostomatous Bryozoa from Vanuatu. *Zoo-*

- logical Journal of the Linnean Society* 131 (1): 35-109.
- VIGNEAUX, M., 1949. Révision des Bryozoaires néogènes du Bassin d'Aquitaine et essai de classification. *Mémoires de la Société Géologique de France*, n.s. 28: 1-153.
- VOIGT, E. & GORDON, D. P., 1998. *Ramicosticella* gen. nov., a new Danian genus of Arachnopusiidae (Bryozoa, Cheilostomatida). *Verhandlungen des Naturwissenschaftlichen Vereins in Hamburg* n.f. 37: 95-104.
- WASS, R. E. & YOO, J. J., 1983. Cheilostome Bryozoa from the Southern Australian Continental Shelf. *Australian Journal of Marine and Freshwater Research* 34: 303-354.
- WINSTON, J. E., 1986. An Annotated Checklist of Coral-Associated Bryozoans. *American Museum Novitates* 2859: 1-39.
- WINSTON, J. E. & HEIMBERG, B. F., 1986. Bryozoans from Bali, Lombok and Komodo. *American Museum Novitates* 2847: 1-49.

Manuscript received 22 December 2003
Revision accepted 21 July 2004